

GROWTH RATES IN THE SCORPION *PSEUDOUROCTONUS REDDELLI* (SCORPIONIDA, VAEJOVIDAE)

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ABSTRACT. Members of the family Vaejovidae are the dominant species of scorpion in much of western North America, yet relatively little is known of the life histories in this group. In this paper I present data on growth rates of a single litter of *Pseudouroctonus reddelli*, a troglomorphic vaejovid from central Texas. From an initial litter of 53 juveniles, one individual reached instar 8. Nearly 75% of this litter died during instar 2 or 3; this mortality rate was quite high, but consistent with other laboratory studies on vaejovid growth. A comparison with adults from this population suggested that *P. reddelli* mature at instar 9 for both males and females. Progression factors for two morphological measures during the early instars were more often below the predicted theoretical value of 1.26, while the progression factor for mass was close to the theoretical value of 2.0. No sexual dimorphism in growth rates was observed for instars 2–4. In comparison with other vaejovids, *P. reddelli* has a larger litter size, shorter instar 1 duration but comparable durations for instars 2–4, and lower morphological progression factors.

The scorpion family Vaejovidae Thorell 1876 is a relatively large group, consisting of at least 150 species (Sissom 1990; Stockwell 1992). Recently, Stockwell (1992) revised the Vaejovidae to include only the nominate subfamily (Vaejovinae Thorell 1876), which includes species distributed from southern Canada through the United States into central Mexico. Although this family contains probably the most studied species of scorpion [*Smeringerus mesaensis* (Stahnke 1957); see Polis 1993 and references therein], relatively little is known of the ecology or life history for the majority of vaejovids. For example, Polis & Sissom (1990) give life history data, such as litter size or number of molts to maturity, for only 18 species.

One of the more interesting vaejovids, both ecologically and taxonomically, is *Pseudouroctonus reddelli* (Gertsch & Soleglad 1972), a relatively large, dark-colored species distributed throughout much of central Texas (Gertsch & Soleglad 1972; Stockwell 1986). As with other vaejovids, individuals may be found under surface debris such as rocks or logs. However, *P. reddelli* is unusual in that it is troglomorphic, with the majority of specimens having been captured from caves (Gertsch & Soleglad 1972; Stockwell 1986)

despite the lack of any obvious adaptations for cave dwelling (such as lack of eyes or pigmentation, or elongated appendages) as seen in troglomorphic scorpions. Individuals are usually located fairly close to the cave entrance (within the initial 50–100 m).

The taxonomic status of *P. reddelli* remains unsettled. It was initially described by Gertsch & Soleglad (1972) as *Vaejovis reddelli* before being transferred to a new genus, *Pseudouroctonus* Stahnke 1974. Subsequent authors (Stockwell 1986; Sissom 1990), noting that characters used to separate *Pseudouroctonus* from *Vaejovis* were not unique to either group, returned *reddelli* to *Vaejovis*. In the most current treatment, Stockwell (1992) has transferred this species, along with species in the *minimus* group of *Vaejovis*, back to *Pseudouroctonus*. I have chosen to utilize this most recent nomenclature while acknowledging that there is still debate both to the validity of *Pseudouroctonus* and the placement of *reddelli* within a genus.

In this paper I analyze growth rates (for both mass and morphometric measures) from a single litter of laboratory-reared *P. reddelli*. These data represent the first life history information for this species, as well as the first data on changes in mass through ontogeny in a laboratory-reared scorpion.

METHODS

Study site.—The female whose litter was used for this study was collected from Kickapoo Caverns State Park, located on the border of Kinney and Edwards Counties approximately 37 km north of Brackettville, Texas. The park lies on the southwestern Edwards Plateau, a region of limestone hills surrounding extensive canyons, dominated by Ashe juniper (*Juniperus ashei*) and plateau live oak (*Quercus fusiformis*) (Lockwood et al. 1993). Underlying the plateau are several underground aquifers which have flowed along major fault lines to create a series of caves and artesian wells (Veni 1988). Within the park, a small population of *P. reddelli* exists in Kickapoo Caverns, a series of chambers near the eastern park boundary. From 1992–1994 a total of seven *P. reddelli* was captured from this cave (6♂, 1♀). No *P. reddelli* have been observed on the surface at the park, where the dominant scorpion species is *Centruroides vittatus* (Say 1821).

Rearing of juveniles.—On 20 July 1993 a single gravid female *P. reddelli* was collected from inside Kickapoo Caverns. This female was found after sunset, approximately 40 m from the cavern entrance along a rock outcropping, by using a portable flashlight with an ultraviolet bulb. Upon return to the laboratory the female was weighed (to the nearest gram), then housed in an 18.5 × 7.5 × 9 cm plastic container with a sand substrate (~ 0.5 cm deep). A wet paper towel was provided to serve as a source of moisture and cover object. The laboratory was maintained on a 14:10 h light:dark photoperiod at a mean temperature of 27.1 °C (range 24–28 °C). The female was fed one adult cricket (*Acheta domestica*) upon return to the laboratory and was offered one adult cricket every three weeks thereafter until giving birth; she was not fed while carrying offspring.

The female gave birth nearly three months after capture, on 10 October 1993. The newborn scorpions (scorplings) oriented themselves in rows on the female's back, as is commonly seen in many species of the genus *Vaejovis* (e.g., Williams 1969). The juveniles molted into instar 2 after 6 days, and dispersed from the female 6–7 days following molting. Immediately after dispersal, each juvenile was individually weighed to the nearest 0.1 mg,

then housed in a 9 cm diameter petri dish containing a small square of paper towel. The petri dishes were stacked and kept in a larger (27.5 × 40 × 16 cm) plastic container with paper towels on the bottom which were moistened daily. This allowed for the maintenance of adequate humidity without having to wet directly the paper towel in each petri dish (excessive watering can drown immature scorpions and hasten growth of mold on uneaten food). Every third day, the top petri dish in a stack was rotated to the bottom to minimize the effect of any moisture gradient within the box. Every third feeding day I transferred each juvenile to a clean petri dish. Following the molt into instar 4 I added a layer of sand 1–2 mm deep to the petri dish. Rearing occurred under the same conditions of temperature and photoperiod as described above.

Juveniles were maintained on hatchling crickets (one week old or less; mean feeding interval = 6.05 days, range 3–10 days), with the number and/or size of the crickets varying with the scorpion's instar. In general, I doubled either the number of crickets or the size of the cricket offered with each increase in instar. Following the molt into instar 6, each juvenile was moved into a container similar to that which housed the female and fed one adult cricket every three weeks.

With the exception of the molt from instar 2 to instar 3 (due to mechanical difficulties with the balance used), juveniles were weighed to the nearest 0.1 mg following each molt. From the exuvium at each molt (or following the death of an individual) I measured three morphological characters [carapace length, metasomal segment V length, and body (prosomal + mesosomal) length] to the nearest 0.01 mm using an American Optical® dissecting microscope equipped with an optical micrometer calibrated at 10×. Body length was computed as the sum of carapace length plus mesosoma length; individual mesosomal segments were not measured separately, as has been recommended by some authors (Stahnke 1970; Sissom et al. 1990). Where possible, I determined sex by looking for the presence of genital papillae, a male secondary sexual characteristic (these were first observed in juveniles during instar 4).

For carapace length, metasomal segment V length, and mass I calculated a progression factor (P.F.) by dividing the value at one instar

by the corresponding value at the preceding instar (e.g., carapace length at instar 4 divided by carapace length at instar 3). Progression factors were then compared to theoretical values (for mass, $PF = 2.0$; for length, $PF = 1.26$, the cube root of 2.0) commonly used to predict the number of molts to maturity in scorpions (reviewed in Francke & Sissom 1984). Finally, I calculated the instar duration as the number of days between successive molts. All statistical analyses were done using the STATISTICA for Windows (vers. 4.5) computer package (StatSoft 1993).

RESULTS AND DISCUSSION

The gravid female had an initial mass of 1250 mg when returned to the laboratory and a mass of 778 mg following offspring dispersal. A total of 53 offspring dispersed from the female; no evidence of cannibalism of juveniles was observed either during birth or while the female carried the offspring. This litter size was relatively high for a vaejovid and is over twice the family average of 23 (Polis & Sissom 1990). Only *V. spinigerus* (Wood 1863), with 66, has a higher reported value (Stahnke 1966). The mean offspring mass following dispersal was 5.8 mg, giving a total litter mass (TLM) of 307 mg. As a measure of reproductive investment by the female I calculated relative clutch mass (RCM) as TLM divided by post-dispersal female mass; this produced a value of 0.395. This represents a lower bound on female investment, as juveniles lose mass while being carried by the female (Formanowicz & Shaffer 1993). This value was below the mean RCMs reported for *Centruroides vittatus* (0.47–0.53, Formanowicz & Shaffer 1993; Brown & Formanowicz 1995), and for *Diplocentrus* sp. and *V. waueri* Gertsch & Soleglad 1972 (0.49 and 0.55, respectively; Brown & Formanowicz 1996).

One individual died following dispersal but prior to the first weighing, leaving 52 juveniles in the initial sample. Of these, 22 molted into instar 3 (42.3% success rate), 14 molted into instar 4 (26.9% success rate), 10 molted into instar 5 (19.2% success rate), four molted into instar 6 (7.7% success rate), two molted into instar 7 (3.8% success rate), and one molted into instar 8. These success rates are low, but comparable to other studies of vaejovid post-birth development (e.g., Francke

1976; Sissom & Francke 1983; Francke & Sissom 1984). Death was usually associated with molting. Occasionally this was due to unknown causes, but more often the molting process had begun while a cricket was in the container, and the juvenile had been preyed upon while helpless during emergence from the old exoskeleton.

The data for the growth rates from this litter of *P. reddelli* are summarized in Table 1. The duration of instar 1 (6 days) is shorter than previously reported for any vaejovid, and is less than half the family mean of 12.6 days (Polis & Sissom 1990). The average duration of instars 2–4 is quite consistent at around 100 days, although substantial variability within an instar does exist, more so in instars 2 and 4 than in instar 3. The duration increases during instars 5 and 6 before decreasing again during instar 7; these values should be regarded with some caution because of lower sample sizes. For the two comparisons for which I had a reasonable (≥ 10) sample size, the duration of time spent in one instar had no effect on the duration of the succeeding instar (Pearson's product-moment correlation: instar 2 vs. instar 3: $r = -0.41$, $P = 0.09$, $n = 18$; instar 3 vs. instar 4: $r = 0.29$, $P = 0.41$, $n = 10$). The durations of instars 2–5 are similar to those reported for *Vaejovis bilineatus* Pocock 1898 (Sissom & Francke 1983) and *Uroctonus mordax* Thorell 1876 (Francke 1976), but considerably shorter than those for *V. coahuilae* Williams 1968 (Francke & Sissom 1984). It should be noted that differences in rearing and feeding regimes existed between my study and these others, primarily in photoperiod and prey; these may strongly affect the growth rates observed (see below and Polis & Sissom 1990).

A bivariate morphometric plot of carapace length versus metasomal segment V length (Fig. 1) showed an overall slight positive allometric relationship. In general, the carapace is longer than metasomal segment V for instars 2–4 and shorter than metasomal segment V for instars 5–8; this pattern appears to be common in vaejovids (Francke 1976; Sissom and Francke 1983; Francke & Sissom 1984). Within an instar, these two characters were not correlated for instar 2 ($r^2 = 0.01$, $P = 0.47$, $n = 47$), but were significantly positively correlated for instar 3 ($r^2 = 0.56$, $P < 0.001$, $n = 20$), instar 4 ($r^2 = 0.80$, $P < 0.001$, $n =$

Table 1.—Growth rates for a single litter of 52 *Pseudouroctonus reddelli*. Data are given as mean \pm SD above, with ranges (sample size n) below. Where there are less than three data points, only the range is given.

Instar	Mass (mg)	Body length (mm)	Carapace length (mm)	Metasomal segment V length (mm)	Duration (days)
2	5.79 \pm 0.51 4.3–7.2 (53)	3.98 \pm 0.75 3.36–6.35 (44)	1.49 \pm 0.05 1.38–1.57 (47)	1.39 \pm 0.04 1.29–1.48 (50)	99.6 \pm 14.1 74–135 (35)
3		4.28 \pm 0.64 3.85–5.95 (17)	1.72 \pm 0.07 1.61–1.84 (20)	1.64 \pm 0.08 1.48–1.80 (21)	103.1 \pm 10.4 87–117 (18)
4	22.5 \pm 3.7 17–31 (12)	5.38 \pm 1.15 4.20–7.64 (14)	1.98 \pm 0.17 1.71–2.26 (14)	1.97 \pm 0.13 1.80–2.21 (14)	97.7 \pm 17.2 69–125 (10)
5	44.8 \pm 11.6 29–69 (10)	8.12 \pm 1.71 5.63–10.28 (9)	2.60 \pm 0.20 2.26–2.93 (9)	2.63 \pm 0.23 2.31–3.04 (10)	154.5 \pm 35.2 107–187 (4)
6	94.2 \pm 16.0 73–111.4 (4)	9.77 \pm 1.83 8.13–12.15 (4)	3.13 \pm 0.24 2.90–3.40 (4)	3.30 \pm 0.24 3.04–3.62 (4)	151–192 (2)
7	201–224 (2)	11.7–15.1 (2)	3.82–4.11 (2)	4.01–4.39 (2)	109 (1)
8	434.4 (1)	18.3 (1)	5.16 (1)	6.08 (1)	

14) and instar 5 ($r^2 = 0.91$, $P < 0.001$, $n = 9$). Carapace length was significantly positively correlated with mass (cube-root transformed to equalize dimensionality with length) within instars 2, 4, and 5 (Figs. 2–4). This relationship is relatively weak initially ($r^2 = 0.12$ for instar 2, $n = 47$), but becomes quite strong during later instars [$r^2 = 0.85$ and 0.96 , respectively, for instar 4 ($n = 12$) and instar 5 ($n = 9$)]. To examine whether there were differences among sexes in growth rates, I performed a series of t -tests using the 15 individuals (9♂, 6♀) for which I was able to identify sex positively. For instars 2–4, the results (Table 2) showed no dimorphism between the sexes in mass, instar duration or morphometric measures, with the exception of metasomal segment V length in instar 4 (females longer than males). Dimorphism among adults in this population may exist, as all of the adult males captured have been larger than the adult female; however, the sample size of adults is far too small to make any definitive statements, and other authors (Gertsch & Sologlad 1972) have described females larger than males.

The mean progression factors (P.F.'s) for carapace length and metasomal segment V length (Table 3) were in general below the theoretical value of 1.26, especially during early development. This was more pronounced for carapace length than for meta-

somal segment V length. These morphological P.F.'s are less than those previously reported for the Vaejovidae. For carapace length and metasomal segment V length, respectively, average P.F.'s were 1.24 and 1.29 for *V. coahuilae* (Francke & Sissom 1984), 1.26 and 1.32 for *V. bilineatus* (Sissom & Francke 1983), and 1.31 and 1.41 for *U. mordax* (Francke 1976). As with these three species, the carapace grows less rapidly (P.F.'s were lower) than does the last metasomal segment in all instars of *P. reddelli*. The mean P.F. for mass (Table 3) was above the theoretical value of 2.0 in three of the four ratios, although sample size was low in all groups. Mass progression factors have not been reported previously for any vaejovid.

The one juvenile to reach instar 8 was a male, as determined by the presence of genital papillae. A comparison of the morphological measurements from this individual (Table 1) to measurements of field-caught *P. reddelli* males suggests that this may be an immature, and thus males may reach sexual maturity at instar 9. Three adult males captured from Kickapoo Caverns in March 1993 had an average carapace length of 6.45 mm and an average metasomal segment V length of 8.22 mm. Both of these measurements are considerably larger than those for the instar 8 individual (Table 1), and would represent progression factors from instar 8 to instar 9 of

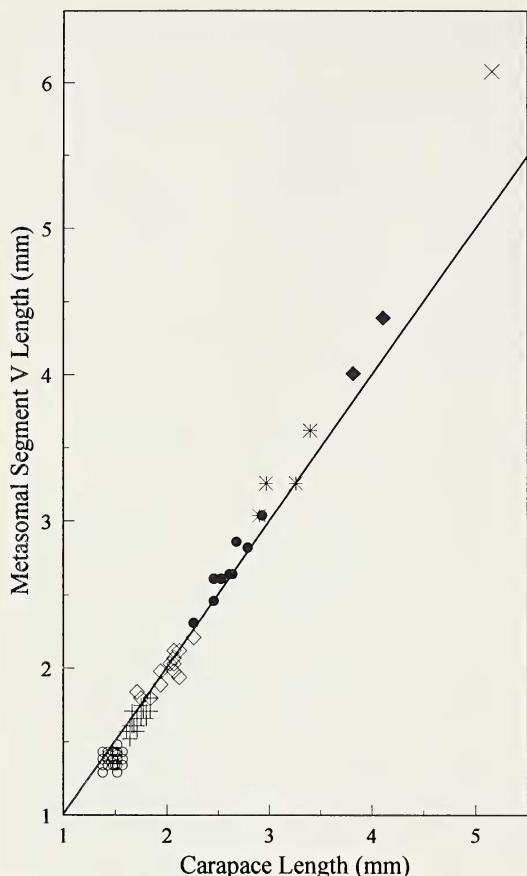
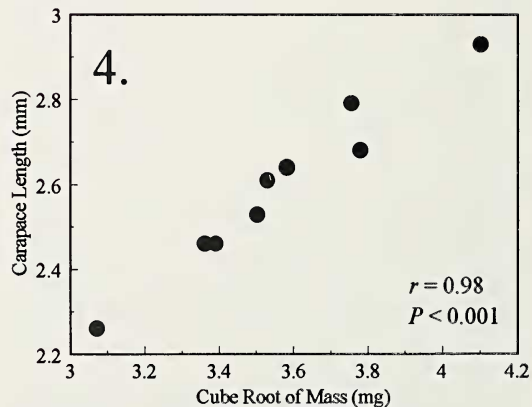
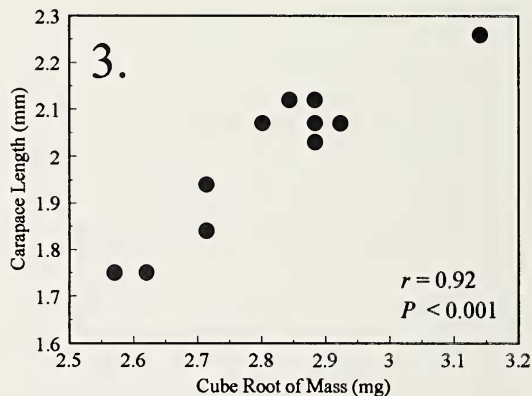
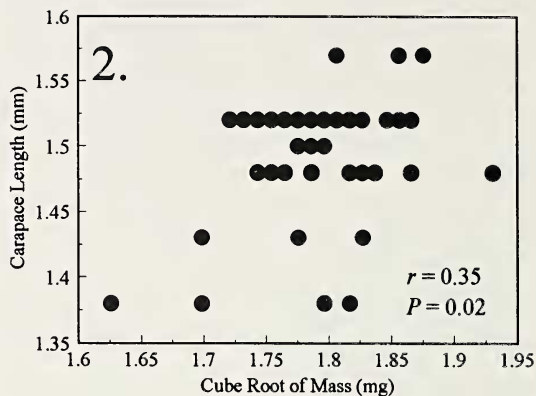


Figure 1.—Bivariate plot of carapace length (in mm) versus metasomal segment V length (in mm) for a single litter of *Pseudouroctonus reddelli*. Symbols are as follows: open circles (○) = instar 2; plus signs (+) = instar 3; open diamonds (◇) = instar 4; closed circles (●) = instar 5; asterisks (*) = instar 6; closed diamonds (◆) = instar 7; crosses (×) = instar 8. The line indicates a 1:1 relationship between the two measures.

1.25 for carapace length and 1.35 for metasomal segment V length. These P.F.'s are within the range of values calculated from earlier instar growth data. Among females from this litter, the two oldest individuals died during instar 5. Using the average P.F.'s from instar 6–8 males (1.22 for carapace length, 1.26 for metasomal segment V length), these females would be expected to reach the adult female's size (carapace length = 6.36 mm, metasomal segment V length = 7.35 mm) at instar 9.

Thus, from the laboratory data it appears that maturity in *P. reddelli* is reached at instar 9 for both sexes. Only two species have pre-



Figures 2–4.—Plots of the cube root of mass (in $\text{mg}^{1/3}$) versus carapace length (in mm) in *Pseudouroctonus reddelli*. r represents the Pearson product-moment correlation between the two variables. 2, Instar 2; 3, Instar 4; 4, Instar 5.

Table 2.—Variation between sexes during instars 2–4 in a subset of 15 individual juveniles (9 males, 6 females) from a litter of *Pseudouroctonus reddelli*. Means are reported for each variable. Within each instar, comparisons were made using a *t* test. ns = not significant. * = significant at $P = 0.05$.

Instar	Sex	Mass (mg)	Carapace length (mm)	Metasomal segment V length (mm)	Duration (days)
2	male	5.95	1.47	1.4	95
	female	5.6	1.5	1.39	97.3
	<i>t</i>	1.31 ns	0.97 ns	0.51 ns	0.28 ns
3	male		1.7	1.64	103.7
	female		1.73	1.67	99.8
	<i>t</i>		0.64 ns	0.88 ns	0.69 ns
4	male	21.4	1.92	1.9	92.4
	female	22	1.99	2.02	98
	<i>t</i>	0.34 ns	0.73 ns	1.88*	0.45 ns

viously been found to require as many instars to reach maturity, both members of the family Diplocentridae Peters 1861: *Didymocentrus trinitarius* (Franganillo 1930) (9–10 instars; Armas 1982) and *Diplocentrus whitei* (Gervais 1844) (8–9 instars; Francke 1982). For the Vaejoidea the mean instar at maturity is 6.8, with a range of 6–8 (Polis & Sissom 1990). At this point I have no evidence to suggest that maturity is reached at different instars, either within a sex or between sexes; this phenomenon has been reported for the vaejovid *V. coahuilae* (Francke & Sissom 1984) as well as a number of species from other families (see Polis & Sissom 1990).

Finally, these results should be viewed with caution, for several reasons. First, as has been

noted by other authors (reviewed in Polis & Sissom 1990), both environmental factors (e.g., temperature) and feeding history can have an influence on traits such as gestation time and growth rates, such that laboratory studies and field studies of scorpion life histories may produce conflicting conclusions for a given species. In this study, this may be the case especially for the estimation of the number of molts to maturity, particularly if progression factors are sensitive to environmental variation (as seems likely). Second, the data presented here represent results from a single litter, so that any genetic variation in reproductive investment patterns (e.g., among individuals or populations) was not uncovered. Third, when comparing these results to those

Table 3.—Progression factors (PF) for carapace length, metasomal segment V length, and mass in *Pseudouroctonus reddelli*. Data are given as mean \pm SD above, range (sample size *n*) below. Where there are less than three data points, only ranges are given.

PF	Carapace length	Metasomal segment V length	Mass
2 \rightarrow 3	1.17 \pm 0.05	1.19 \pm 0.05	
	1.09–1.29 (20)	1.10–1.28 (21)	
3 \rightarrow 4	1.15 \pm 0.07	1.18 \pm 0.06	
	1.00–1.23 (14)	1.11–1.29 (14)	
4 \rightarrow 5	1.29 \pm 0.03	1.35 \pm 0.05	2.03 \pm 0.21
	1.26–1.34 (9)	1.28–1.45 (10)	1.71–2.35 (9)
5 \rightarrow 6	1.22 \pm 0.07	1.27 \pm 0.04	2.23 \pm 0.21
	1.13–1.28 (4)	1.23–1.32 (4)	2.04–2.52 (4)
6 \rightarrow 7	1.17–1.21 (2)	1.21–1.23 (2)	2.01–2.04 (2)
7 \rightarrow 8	1.26 (1)	1.38 (1)	1.94 (1)

from other studies on scorpion growth, it is important to take strongly into account differences in rearing and feeding conditions, whether the study was field- or lab-based, and whether individuals from various populations were used, since all of these factors are potential influences on variation in scorpion growth and reproduction.

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